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Soil and season shape less intensively managed agro-ecosystems of a Mediterranean island—Insights from Lemnos (Greece)

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Abstract

Aims: This study presents a novel characterization of agrestal plant communities associated with traditional, less intensively managed Mediterranean agro-ecosystems, focusing on the influence of seasonal phases, soil-, and land-use conditions, and the presence of obligate arable plant species. **Study area:** The island of Lemnos, North Aegean. **Methods:** The vegetation was recorded in spring and fall. We sampled 174 plots located in fields cultivated with cereals and pulses and in fallow and stubble fields across the island. We used non-metric multidimensional scaling (NMDS) to analyze compositional patterns and identify differences between seasons. NMDS and modified TWINSPAN clustering were applied to spring plots to distinguish plant communities and their differential species. Edaphic and other environmental influences were evaluated using a geological map and ecological indicator values. The frequency and distribution of obligate arable plant species were also assessed. **Results:** Fall vegetation was dominated by late-flowering annuals, biennials, and perennials colonizing fields after harvest. In spring, four distinct spring plant assemblages were identified in fields of winter cereals and pulses, structured along soil gradients ranging from acidic sandy to base-rich loamy soils and from dry to temporarily wet soils. Crop type and fallowing were also found to influence community structure. The island supports a high number of obligate arable species, including several threatened ones. **Conclusion:** Our findings highlight the ecological and botanical importance of Lemnos' less intensively farmed agricultural landscape. Soil heterogeneity and seasonal phases promote considerable species and community diversity, resources for wildlife, and the persistence of specialized and rare arable plant species. In the face of increasing agricultural intensification across Europe, the conservation value of less intensive agro-ecosystems is evident. Lemnos offers a rare opportunity to preserve segetal biodiversity *in situ*.

Taxonomic reference: Euro+Med (2006-).

Syntaxonomic reference: Mucina et al. (2016).

Abbreviations: EIVE = Ecological Indicator Values for Europe; IUCN = International Union for Conservation of Nature; LC = Least Concern (Red List category); NT = Near Threatened (Red List category); NMDS = Non-metric Multi-Dimensional Scaling; PERMANOVA = Permutational Multivariate Analysis of Variance; PERMDISP = Permutational Multivariate Analysis of Dispersion; TWINSPAN = Two-Way Indicator Species Analysis; VU = Vulnerable (Red List category).

Keywords

Aegean, agrestal, agro-ecosystem, arable, biodiversity, conservation, Greece, plant community, season, segetal, soil, vegetation

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Introduction

Between 12,000 and 10,000 years ago, humans began transitioning from a nomadic foraging way of life to permanent settlements, animal domestication, and agriculture. This Neolithic transition originated in the Fertile Crescent of Southwest Asia and spread into Europe through Greece (Zeder 2008). The earliest agricultural remains in Greece can be dated back to around 9,000 to 8,500 years ago (Allen 2018; Isaakidiu et al. 2022).

The advent of agriculture transformed landscapes by creating or modifying open habitats subject to frequent and regular soil disturbance. Some wild plant species were selected and domesticated as crops while other ruderal plant species assembled and co-evolved alongside them, resulting in the emergence of new agrestal (i.e., wild arable) plant communities (Zohary 1950; De Wet and Harlan 1975; Meyer et al. 2012). The composition of these arable plant communities is shaped by a combination of land management practices (e.g., crop type, type and intensity of tillage, rotation practices, use of irrigation, herbicides, fertilizers, and grazing), abiotic factors (e.g., territory, soil characteristics, nutrient availability, and precipitation), and temporal variation such as seasonality (Zimdahl 2007; Fried et al. 2008; Cordeau et al. 2017; Friedrich 2020; Bopp et al. 2022).

The island of Lemnos in the northeastern Aegean archipelago has been inhabited at least since the Neolithic due to its favorable geographic location (Efstratiou et al. 2014; Triantaphyllou et al. 2023; Thomas et al. 2024). It is historically known for its fertile plains and cultivable soils, which are valuable for agricultural production (Kizos and Vlahos 2012; Dimopoulos et al. 2018). Consequently, crops were selected and cultivated to fit the island's environmental conditions for thousands of years, resulting in a number of local landraces (Thanopoulos and Bebeli 2024). The associated arable plant species have adapted accordingly (De Wet and Harlan 1975). To this day, arable fields cover a substantial part of Lemnos, and the amount of agricultural land remains relatively stable (Dimopoulos et al. 2018).

Agriculture on Lemnos primarily involves the cultivation of winter-annual cereals, mostly used as fodder crops, typically managed in mixed intercropping systems and with crop rotations. These are often followed by fallowing or seasonal grazing, creating a unique and complex system of less intensive agriculture and livestock farming on the island, which has largely disappeared elsewhere (Dimopoulos et al. 2018; Georgiadis et al. 2022).

Agriculture with less intensive methods supports high farmland biodiversity and an abundance of native and archaeophytic arable plant species (van Elsen 2000; Bengtsson et al. 2005; Hoffmann and Wahrenberg 2021). In particular, winter cereal fields are among the most valuable habitats for wild arable plant diversity (Bergmeier and Meyer 2018).

However, less intensive agriculture has become rare in Europe and the Mediterranean (Storkey et al. 2012). On Lemnos, many traditional farms (*mandras*) and marginally terraced fields are abandoned. This development is reinforced by the shift toward intensified farming on more fertile land (Margaris 1992; Kizos and Vlahos 2012; Dimopoulos et al. 2018). Because many arable plants depend on disturbance by less intensive farming, both abandonment and intensification contribute to biodiversity loss (Storkey et al. 2012; Hoffmann and Wahrenberg 2021). Understanding the characteristic species composition, land-use characteristics, seasonal variation, and abiotic constraints of arable plant communities is therefore essential for their conservation.

Our study builds on data collected in the framework of the Terra Lemnia project, which aimed to preserve the island's traditional agricultural landscape and to support its products, landraces, farmland biodiversity, and sustainable management practices (MedINA 2021). We compare our findings to the syntaxonomic framework of Mucina et al. (2016), where the class *Papaveretea rhoeadis* represents typical Eurasian winter-annual arable plant vegetation. These habitats are recognized in the EUNIS system as "Arable land with unmixed crops grown by low-intensity agricultural methods" (Schaminée et al. 2012, p. 86) and are listed as Endangered in the European Red List of Habitats (Janssen et al. 2016).

Because agriculture on Lemnos includes rotational fallowing and stubble fields, features of historical land use that have largely disappeared in much of Europe, our study offers the unique opportunity to include the vegetation of such fields. This allows for a broader understanding of arable plant diversity and historical agricultural landscape characteristics that often go unnoticed when considering cereal fields alone.

Despite their ecological importance, agrestal plant communities in Greece remain understudied, and detailed analyses of their composition and habitat conditions are lacking (Meyer and Bergmeier 2020). We want to contribute to closing this gap by describing the agrestal plant communities of Lemnos, focusing on local distribution, ecological preferences, and land-use requirements. In addition, we place the local arable plant communities in a biogeographical context of vegetation alliances to enable a comparison with other Mediterranean vegetation descriptions. Specifically, we aim to:

1. Identify and characterize the arable plant communities of Lemnos and their differential and diagnostic species.
2. Analyze the distribution of these communities across the island in relation to abiotic environmental factors and land-use conditions.
3. Investigate the occurrence of obligate threatened arable plant species in Greece, identified by Bergmeier and Strid (2014), and assess what is needed for the conservation of those species that occur almost exclusively on arable fields.

Study area

Lemnos, the ninth-largest Greek island, spans approximately 480 km^2 and is situated in the northeastern Aegean Sea (Dimopoulos and Kizos 2020). It is located in the southern part of the North Aegean Islands floristic region, as defined by Strid and Tan (1997). Lemnos is geographically isolated from the other North and Northeast Aegean Greek islands of Thasos, Samothraki, and Lesvos and the Turkish island of Gökçeada (Imvros), as

well as from the Greek and Turkish mainland (Panitsa et al. 2003). This isolation, combined with its location within the Aegean biodiversity hotspot (Médail and Quézel 1997), contributes to its ecological richness and singularity.

Lemnos has a Mediterranean climate with hot, dry summers and mild, wet winters and is subject to strong northern and northwestern winds. The annual mean temperature in the capital, Myrina, is 16.6 °C, with average annual precipitation of approximately 500 mm (Climate-Data.org 2022).

The island lies in a tectonically active zone, but volcanic activity is limited to the past and occurred during the Upper Oligocene and Lower Miocene. As a result, volcanic rocks (andesites, dacites, and trachytes) and tuffs cover about 30% of the island, producing shallow, stony soils. Deeper soils are found in alluvial and coastal deposits, which account for around 15%. Eocene-Oligocene molasse sedimentary rocks (conglomerates, clay-, and sandstone) cover roughly half of the island's surface. There are also minor occurrences of Miocene and Pleistocene deposits, mainly conglomerates, calcareous sandstone, marls, and marly limestone. Soil carbonate content varies depending on bedrock: volcanic areas are typically acidic and low in carbonates, whereas alluvial deposits, marls, and sedimentary rocks often yield soils with poor to moderate carbonate levels (Figure 1; IGME 1993; Kosmas et al. 2024).

Compared to other Greek islands, Lemnos features a relatively gentle topography, which is likely due to the absence of metamorphic calcareous rocks. The landscape is divided between stony uplands in the west, peaking at 429 m a.s.l., and fertile lowlands in the central and eastern parts. The island is characterized by phrygana (Aegean low shrubland), grasslands, wetlands, sandy flats, and coastal rocks and dunes, as well as agricultural fields. Woodlands and macchia (tall shrublands) are scarce (Panitsa et al. 2003; Georgiadis et al. 2022; Thomas et al. 2024).

The contrasting relief of the island results in different land-use practices. In the hills, a combination of livestock farming and agriculture is practiced, while the plains and foothills are characterized by a farmland mosaic dominated by viticulture and the cultivation of (rain-fed) fodder and staple crops such as barley, oat, wheat, pulses, and sesame (Dimopoulos and Kizos 2020; Thomas et al. 2024). Intercropping of mixed cereals, particularly barley and oat (Figure 2A), and more rarely fodder pulses (common vetch and pea), among others, is practiced to buffer climatic variability: barley tends to perform better in dry years, while oat thrives under wetter conditions. Crop rotation is common, alternating cereals with pulses and/or fallows to rest the land (Figure 2B); the sequence varies by farm. Cereals are sown between November and January and mainly harvested for hay in May. Some fields are grazed green by sheep and other livestock, while others are left to grow for seed production (Figure 2C–E). While the number of individual farmers and *mandras* is decreasing (Figure 2F), land consolidation results in fewer farmers managing larger areas. Partial intensification is evident, including increased use of synthetic fertilizers and herbicides.

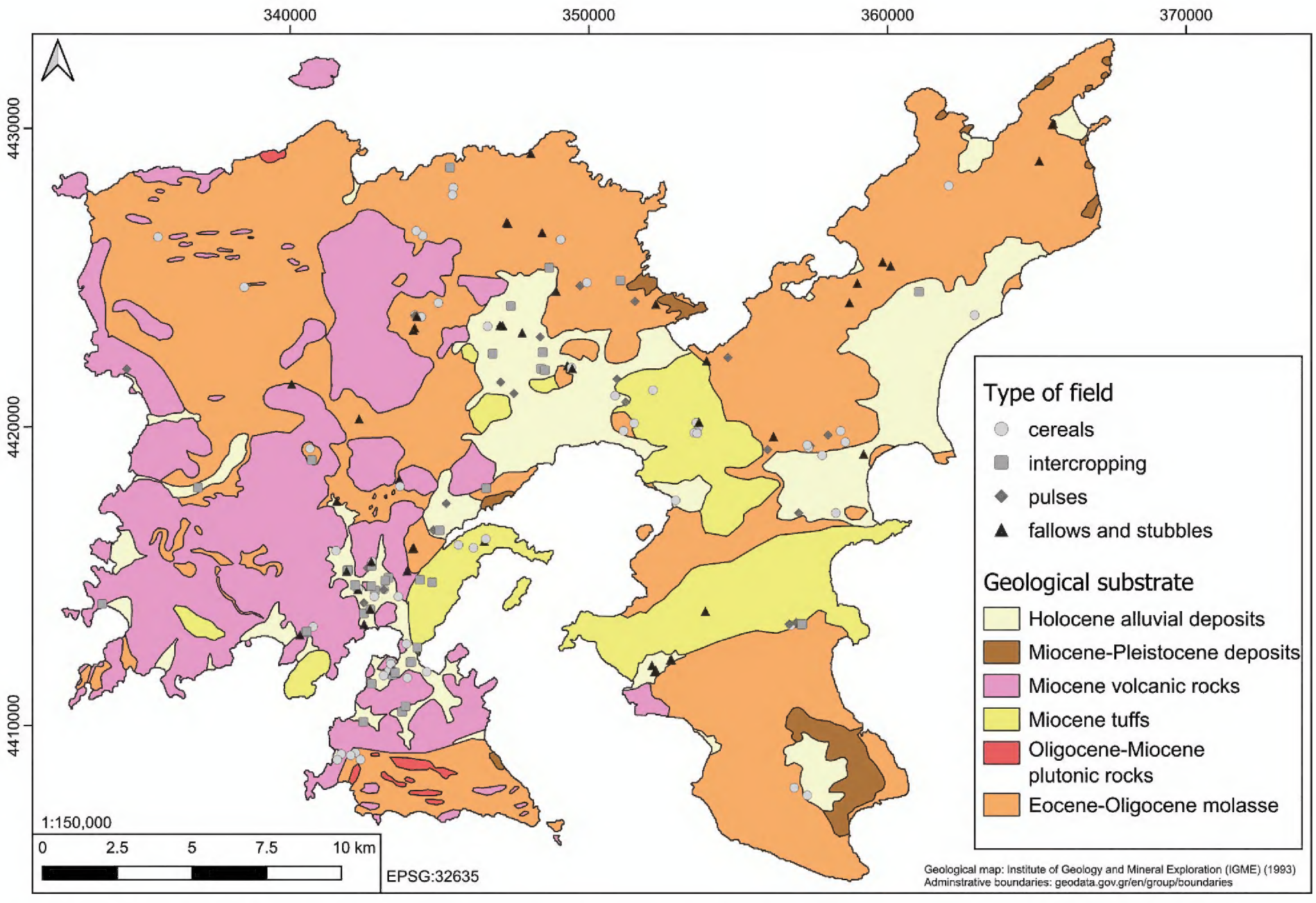

Figure 1. Map of the island of Lemnos depicting the geological substrates based on the geological map from the IGME (1993), and the type of field (cereals, intercropping, pulses, fallows and stubble fields) of the 174 sampled fields.

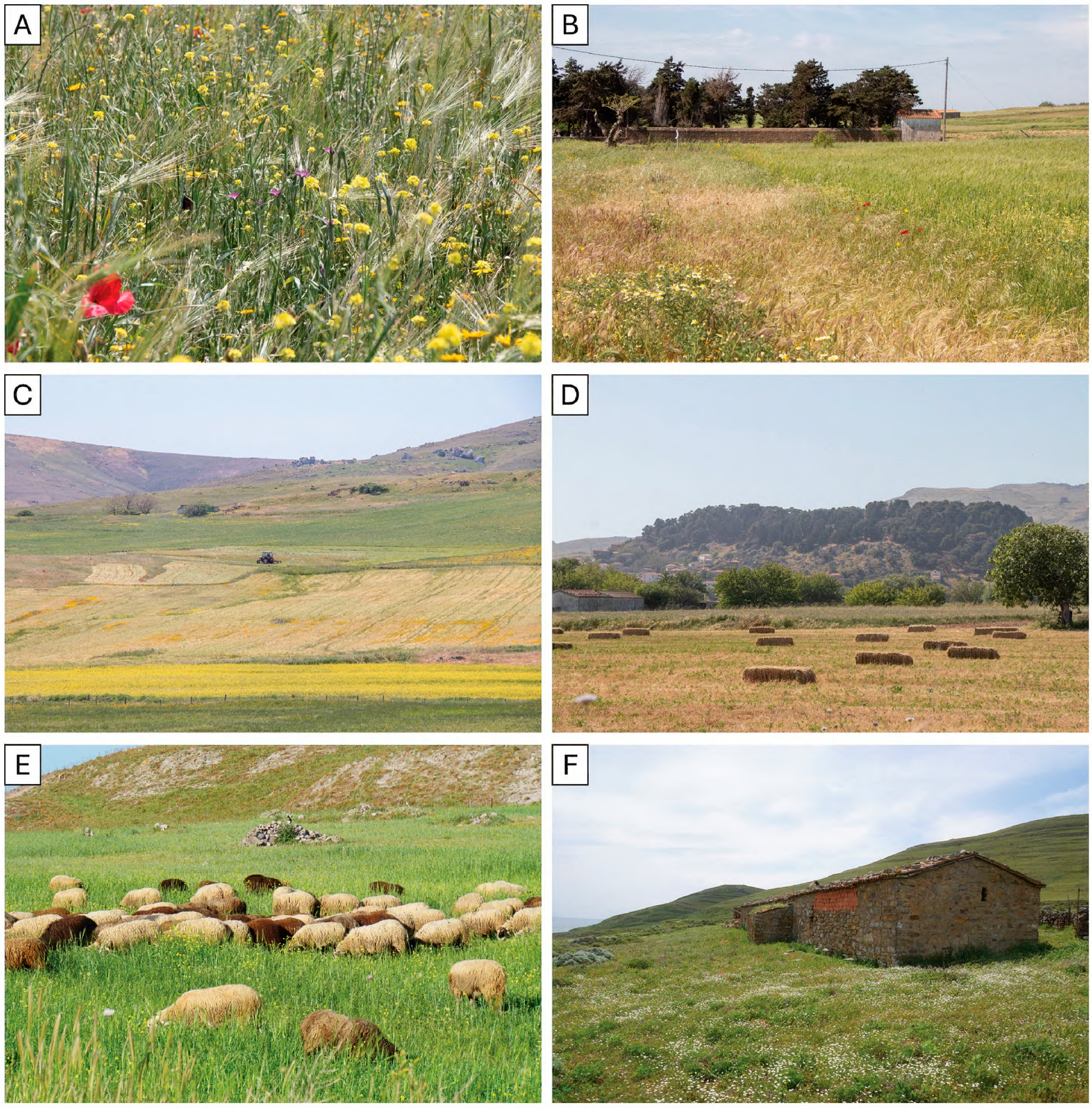

Figure 2. Photographs from Lemnos. A: Field intercropped with *Hordeum vulgare* (barley) and *Avena sativa* (oat) including *Agrostemma githago*; B: Rotational fallow (left) adjacent to a cultivated field (right); C: Hay harvest on Fakos peninsula; D: Hay bales; E: Grazing sheep; F: Abandoned *mandra*. Photos A–D: L. Rinne; E-F: S. Meyer.

Methods

Data acquisition

We collected the data as part of the Terra Lemnia Project (MedINA 2021) between 2018 and 2022, with additional sampling conducted in May 2025, targeting underrepresented field types such as pulses. We based our analysis on 174 plots: 130 were recorded in spring (April and May) and 44 in fall (September and October). Only one plot was recorded per field. The surveys were conducted on mostly 100 m^2 plots ([25–]100[–150] m^2) located within field interiors.

We estimated the plant species cover and abundance using the nine-part Braun-Blanquet scale (Wilmanns 1989). The crop species were also recorded. Cereal crops included, in the order of frequency encountered, Six-rowed Barley (*Hordeum vulgare*), Oat (*Avena sativa*), Pasta Wheat (*Triticum durum*), Two-rowed Barley (*Hordeum distichon*), Triticale (*Triticosecale*), and Bread Wheat (*Triticum aestivum*). Pulse crops included Common Vetch (*Vicia sativa*), Garden Pea (*Pisum sativum*), Broad Bean (*Vicia faba*), Lentil (*Lens culinaris*), Pale Pea (*Lathyrus ochrus*), and Black-eyed Bean (*Vigna unguiculata*).

In addition, we recorded geographic coordinates and habitat characteristics, such as total vegetation cover, crop cover, altitude, fine soil proportion, and soil stoniness (skeletal fraction). Fields with apparent herbicide application were not included. Assuming reduced species numbers, fields with more than 95% crop cover and less than 10% herbaceous wild arable plant cover were classified as heavily fertilized and were not included.

Statistical and spatial analysis

The plots were digitized using Turboveg 2 (Hennekens and Schaminée 2001). All statistical and spatial analyses were performed in R version 4.4.2 (R Core Team 2024) within the RStudio environment (RStudio Team 2025). The script and data frames are provided as Suppl. material 1. For data preparation, handling, and plotting, we used 'tidyverse' (Wickham et al. 2019) with the addition of 'ggradar' (Bion 2025) for radar charts. Maps were created with QGIS (QGIS Development Team 2024). Plant family information was derived with the package 'taxize' (Chamberlain and Szöcs 2013) based on the National Center for Biotechnology Information database.

All multivariate analyses were conducted using 'vegan' (Oksanen et al. 2024). To minimize the influence of sown crop species on the analysis, observations of crops with a cover above 1 on the nine-part Braun-Blanquet scale were excluded. Observations identified only at the genus or family level were also removed, retaining species and subspecies for ordination and clustering. We calculated a 2-dimensional Non-Metric Multidimensional Scaling (NMDS) for the whole dataset with untransformed data (distance measure = Bray-Curtis). Plots were grouped by season. We assessed group dispersion homogeneity (PERMDISP; Anderson 2006) before conducting a permutational multivariate analysis of variance (PERMANOVA; McArdle and Anderson 2001) to test for significance. We identified species associated with spring or fall with the package 'goeveg' (von Lampe and Schellenberg 2024) by creating a synoptic table (frequency threshold = 20%).

For a more detailed analysis of the spring communities, the 130 spring plots were analyzed separately. To identify vegetation clusters, we used the package twinspanR (Zelený 2021) with the modified TWINSPAN algorithm (Roleček et al. 2009) under default settings (five pseudospecies cut levels = 0%, 2%, 5%, 10%, 20%; dissimilarity measure = total inertia). We explored different cluster numbers and selected four clusters based on their ecological interpretability via diagnostic species and associated environmental parameters. A synoptic table was created with 'goeveg' (frequency threshold = 25%) to compare species composition among clusters. Additionally, species fidelity was assessed by calculating their differential character following the approach of Tsiripidis et al. (2009) using the 'goeveg' package. Based on percentage frequency, species were classified as positively or negatively differentiating for one or several groups, or as indifferent. Dominant species were defined as non-crop taxa reaching cover values ≥ 3 on the nine-part Braun-Blanquet scale in at least five relevés. The synoptic table was sorted by percentage frequency and differential character of species related to a certain community, main group, several, or no groups.

To evaluate ecological conditions, we applied Ecological Indicator Values for Europe (EIVE; Dengler et al. 2023), which are based on the Ellenberg system and include values for moisture, reaction, nitrogen, light, and temperature. Community-weighted means (CWMs) for each indicator were calculated per plot and visualized as boxplots for the four spring and the fall communities. Additionally, we calculated a 3-dimensional NMDS (untransformed data; distance measure = Bray-Curtis) of only the spring dataset to explore the vegetation patterns by fitting the CWMs of the indicator values post hoc into the ordination space using the package 'weimea' (Zelený 2018).

We compared species richness between spring and fall communities using a pairwise Wilcoxon rank-sum test with Holm correction due to non-normal data distribution. Additionally, mean species richness per field type was assessed separately for each season. We digitized the geological map of Lemnos (IGME 1993) in QGIS. Geological substrates were grouped into six categories: 1) Holocene alluvial deposits; 2) Miocene-Pleistocene deposits; 3) Miocene volcanic rocks; 4) Miocene tuffs; 5) Oligocene-Miocene plutonic rocks; and 6) Eocene-Oligocene molasse. To assess the influence of geological substrate, we spatially joined the plots with the geological map by employing the package 'sf' (Pebesma 2018). The influence of field type and geological substrate on plant communities was tested using a Chi-squared test.

Obligate agrestal plant species assessment

Bergmeier and Strid (2014) identified obligate arable plant species of Greece and determined their conservation status according to International Union for Conservation of Nature (IUCN) Red List criteria. Their publication served as a basis to evaluate the richness and frequency of obligate arable plant species on Lemnos with a special focus on species classified as Vulnerable (VU) and Near-threatened (NT).

To examine their local populations, we quantified the frequency of each obligate wild arable plant species recorded on the island. Furthermore, we calculated the mean number of obligate and threatened arable species per cluster, allowing us to assess the potential of each vegetation cluster to support these species.

Results

Seasonal variation in plant community composition

A clear seasonal distinction in species composition was observed between spring and fall communities (Figure 3). PERMANOVA confirmed a significant effect of season on community composition ($F = 30.168$; $df = 1$, $R^2 = 0.149$; $p < 0.01$), and PERMDISP indicated no significant difference ($F = 0.319$; $p = 0.539$), confirming that observed seasonal differences were driven by species composition rather than heterogeneity.

Spring plots were associated with early flowering annual plant species such as *Lolium rigidum*, *Anagallis arvensis*, *Papaver rhoeas*, *Raphanus raphanistrum*, *Anthemis cotula*, *Scandix pecten-veneris*, *Rapistrum rugosum*, *Sinapis arvensis*, *Lolium temulentum*, *Agrostemma githago*, *Herniaria hirsuta*, *Glebionis segetum*, and *Anchusa hybrida* (Table 1).

The stubble field plant assemblages were dominated by late-flowering annuals, such as *Dittrichia graveolens* and

Table 1. Shortened synoptic table (frequency threshold = 20%) depicting the percentage frequency of species associated with spring and fall communities sorted by percentage frequency. The full synoptic table and species matrix are available in Suppl. material 2.

Number of plots	Spring 130	Fall 44
Species associated with spring communities		
Lolium rigidum	86	14
Anagallis arvensis	83	30
Papaver rhoeas	75	0
Raphanus raphanistrum	70	5
Sonchus asper subsp. *glaucescens*	62	36
Anthemis cotula	60	2
Rapistrum rugosum	52	14
Melilotus indicus	50	5
Scandix pecten-veneris	46	2
Matricaria chamomilla	43	5
Sinapis arvensis	42	2
Lolium temulentum	40	5
Agrostemma githago	38	0
Herniaria hirsuta	38	0
Glebionis segetum	37	0
Vicia lutea	36	0
Lathyrus aphaca	35	0
Silene gallica	33	0
Anchusa hybrida	32	9
Galium tricornutum	30	0
Filago pyramidata	28	9
Ammi majus	27	11
Phalaris paradoxa	25	2
Ranunculus marginatus	25	0
Torilis nodosa	25	2
Papaver hybridum	24	0
Hypecoum imberbe	22	0
Polygonum aviculare	22	2
Sonchus oleraceus	22	2
Vicia sativa	21	0
Species associated with fall community		
Dittrichia graveolens	1	91
Centaurea solstitialis	20	68
Heliotropium europaeum	0	68
Dittrichia viscosa	4	61
Polygonum arenarium	31	57
Hypericum triquetrifolium	20	41
Cichorium intybus	18	39
Chrozophora tinctoria	0	30
Kickxia elatine subsp. *crinita*	0	30
Cynodon dactylon	3	25
Salsola squarrosa	2	25
Chondrilla juncea	7	23
Daucus carota	8	23
Symphyotrichum squamatum	0	23
Chenopodium betaceum	1	20
Species associated with spring and fall		
Convolvulus arvensis	32	27
Hirschfeldia incana	32	23
Rumex pulcher	30	23

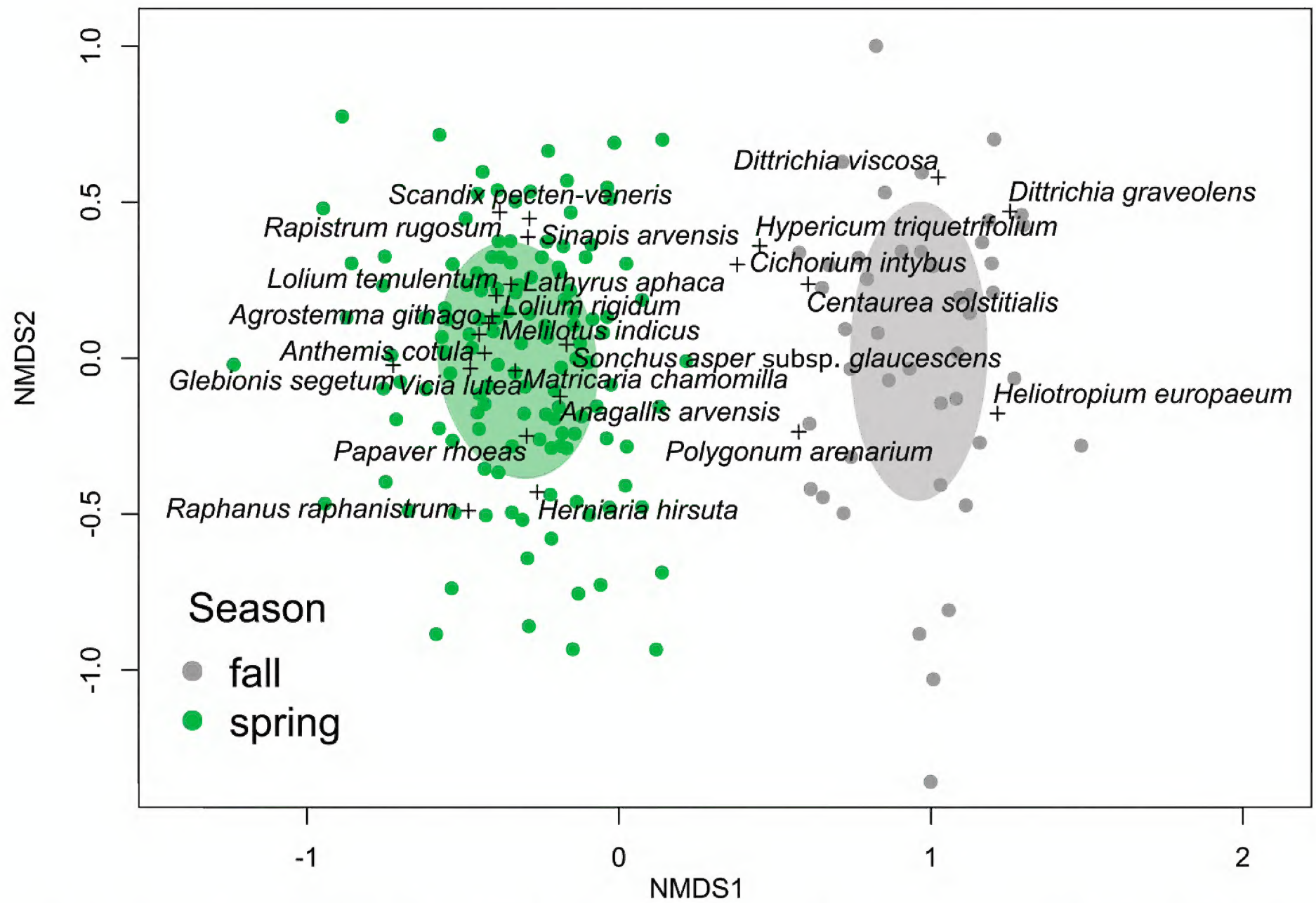

Figure 3. Two-dimensional NMDS ordination of the full dataset (stress = 0.212), showing a clear separation between spring and fall plots (PERMANOVA, $p < 0.01$). Ellipses represent standard deviation around the centroid of each cluster. Species with ≥ 33% frequency in either season were fitted post hoc, and their positions indicate associations with seasonal groups.

Heliotropium europaeum, as well as biennials, and perennials (*Dittrichia viscosa*, *Centaurea solstitialis*, *Hypericum triquetrifolium*, and *Cichorium intybus*) (Table 1). These species typically germinate or rosulate in spring and flower and fruit in summer and fall, mainly in stubble fields. Adaptations such as basal rosettes (e.g., *Cichorium intybus*, *Centaurea solstitialis*), prostrate growth (e.g., *Polygonum arenarium*, *Cynodon dactylon*), or procumbent branches attached low to the stems (e.g., *Chrozophora tinctoria*, *Dittrichia graveolens*, *Chondrilla juncea*) reduce damage from harvest.

Species with persistent vegetative structures were found at similar frequencies in both seasons, such as geophytes with root suckers (e.g., *Convolvulus arvensis*), perennials with taproots (e.g., *Rumex pulcher*), and annuals capable of resprouting (e.g., *Hirschfeldia incana*).

Classification and description of spring plant communities

TWINSPAN analysis of the spring dataset identified two main groups, each subdivided into two vegetation clusters, resulting in four distinct arable plant communities in winter crop fields (Table 2; Figure 4). The groups can be characterized by species composition, differential character of species, species richness, main crop type, and soil characteristics.

The differential species of the first main group (clusters 1 and 2) were *Anchusa hybrida*, *Herniaria hirsuta*, *Papaver hybridum*, *Polygonum arenarium*, and *Anthemis auriculata*. Conspicuous was the pale-yellow flowering of the dominant species *Raphanus raphanistrum*, an indicator for acidic soils, in many fields of the first main group.

Cluster 1: *Anchusa hybrida-Hypecoum imberbe* community (Figure 4A). The first cluster (38 plots) was characterized by the positively differentiating species *Hypecoum imberbe*. Apart from the prominent flowering aspect of *Raphanus raphanistrum*, the bluish-violet flowering *Anchusa hybrida* was often dominant, especially on young fallows. Speirochorous (sown with crop seed) species (e.g., *Agrostemma githago*, *Lolium temulentum*) had a low frequency (Table 2), probably due to a high proportion of rotational fallows and pulse fields associated with the plant community. The associated coarse sandy soils, derived from Eocene-Oligocene molassic sediments, were well-drained, dry, and unproductive, indicating a tolerance for rather humus-poor soils.

Cluster 2: *Raphanus raphanistrum-Cladanthus mixtus* community (Figure 4B). The second cluster (20 plots) showed a preference for fields with sandy and loamy, acidic, base-poor, and partly seasonally wet soils. Typical positively differentiating species included indicators for temporarily wet, sandy soils, such as *Juncus bufonius* and *Spergula arvensis*.

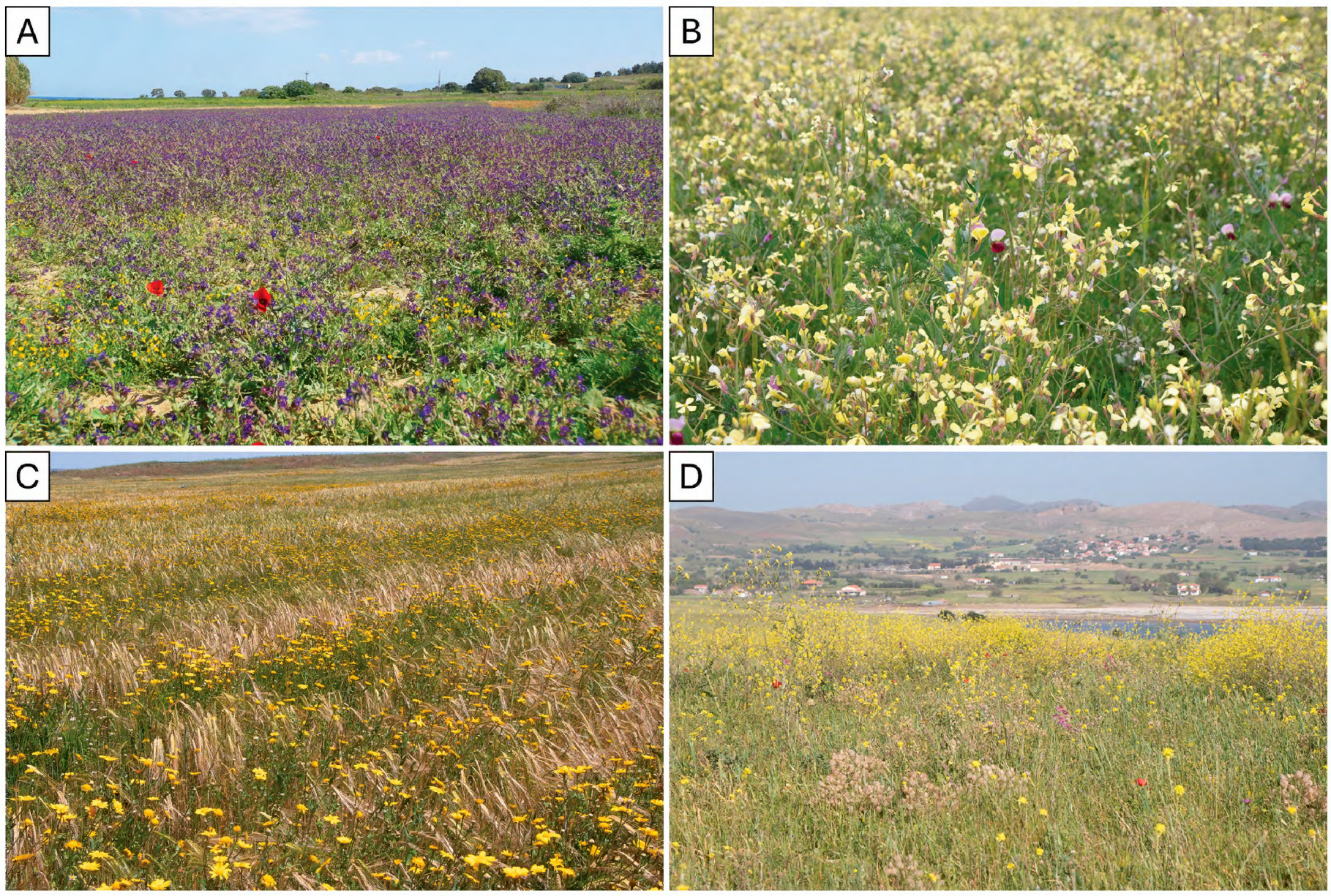

Figure 4. Photographs of the arable plant communities identified on Lemnos in spring. A: *Anchusa hybrida-Hypecoum imberbe* community on a rotational fallow; B: *Raphanus raphanistrum-Cladanthus mixtus* community within a pea (*Pisum sativum*) field; C: *Glebionis segetum-Ranunculus marginatus* community within a barley (*Hordeum distichon*) field; D: *Hypericum triquetrifolium-Leontice leontopetalum* community with *Gladiolus italicus* in a barley field. Photo A: S Meyer; B–D: L. Rinne.

Table 2. Shortened synoptic table (frequency threshold = 25%) depicting the percentage frequency of species associated with the four spring communities (AncHyp: *Anchusa hybrida-Hypecoum imberbe*; RapCla: *Raphanus raphanistrum-Cladanthus mixtus*; GleRan: *Glebionis segetum-Ranunculus marginatus*; HypLeo: *Hypericum triquetrifolium-Leontice leontopetalum*). The differential character is indicated by shading with positively differentiating species in dark grey, negatively differentiating species in light grey, and indifferent species in white. The full synoptic table and species matrix are available in Suppl. material 3.

Number of plots	AncHyp 38	RapCla 20	GleRan 45	HypLeo 27
***Anchusa hybrida-Hypecoum imberbe* community**				
Hypecoum imberbe	66	10	2	0
***Raphanus raphanistrum-Cladanthus mixtus* community**				
Juncus bufonius	16	50	18	0
Cladanthus mixtus	16	45	7	4
Hordeum murinum	13	45	13	4
Spergula arvensis	0	45	2	0
Hypochaeris radicata	0	40	7	4
Ornithopus compressus	0	25	0	0
***Glebionis segetum-Ranunculus marginatus* community**				
Ranunculus marginatus	8	0	56	15
Helminthotheca echioides	5	0	33	11
***Hypericum triquetrifolium-Leontice leontopetalum* community**				
Sinapis arvensis	26	15	44	78
Hypericum triquetrifolium	18	0	0	70
Lathyrus aphaca	18	15	38	70
Leontice leontopetalum	5	0	0	63
Rumex pulcher	13	5	36	63
Bifora testiculata	0	0	13	52
Silene vulgaris subsp. *macrocarpa*	24	5	0	52
Anagallis foemina	13	0	2	44
Rhagadiolus stellatus	0	0	2	44
Cichorium intybus	21	5	9	41
Notobasis syriaca	5	10	0	41
Anisantha madritensis	16	5	4	37
Centaurea solstitialis	24	5	13	37
Plantago lagopus	16	15	4	37
Buglossoides arvensis	13	0	2	30
Gladiolus italicus	0	0	0	30
Medicago scutellata	8	0	9	30
Diagnostic species for the first main group				
Herniaria hirsuta	76	50	18	11
Anchusa hybrida	74	40	2	15
Polygonum arenarium	50	50	22	4
Papaver hybridum	50	25	2	22
Anthemis auriculata	26	40	2	0
Diagnostic species for the second main group				
Rapistrum rugosum	26	5	82	74
Anthemis cotula	45	25	82	70
Scandix pecten-veneris	18	0	69	81
Lolium temulentum	13	35	58	52
Glebionis segetum	11	35	56	44
Vicia lutea	16	10	56	52
Galium tricornutum	8	5	38	67
Ammi majus	13	5	38	44
Torilis nodosa	3	0	33	63
Sherardia arvensis	0	15	22	44
Calendula arvensis	0	0	24	37
Diagnostic species for several groups				
Melilotus indicus	61	5	47	74
Filago pyramidata	26	40	9	52
Matricaria chamomilla	26	70	60	19
Polygonum aviculare	18	35	31	0
Frequent species without differential character				
Papaver rhoeas	100	45	67	78
Anagallis arvensis	84	80	80	89
Raphanus raphanistrum	76	85	73	44
Sonchus asper subsp. *glaucescens*	50	40	67	85
Lolium rigidum	74	90	87	100
Agrostemma githago	24	30	62	26
Hirschfeldia incana	42	30	18	44
Silene gallica	16	40	51	22
Convolvulus arvensis	18	20	40	44
Phalaris paradoxa	18	20	33	22
Sonchus oleraceus	13	15	36	15
Vicia sativa	11	10	31	26
Trifolium campestre	8	25	16	22
Carduus pycnocephalus	11	25	11	22
Ranunculus muricatus	5	10	27	7

Anthemoid species such as *Cladanthus mixtus*, *Anthemis auriculata*, and *Matricaria chamomilla* shaped the flowering aspect together with *Raphanus raphanistrum* (Table 2).

The community shared differential species with cluster 3, such as *Matricaria chamomilla* and *Polygonum aviculare*, indicating preferential similarities of the two community types for mesic, wet-dry soils. Characteristically was also the absence of indicator species for alkaline soils, such as *Bifora testiculata*, *Rhagadiolus stellatus*, or *Scandix pecten-veneris*. Fields of the *Raphanus raphanistrum-Cladanthus mixtus* community were chiefly found near the villages of Kontias in the southwest of the island, Atsiki in the center, and the Kalliopi-Kontopouli area in the east (Figure 5).

The second main group (clusters 3 and 4) shared several differential species linked to more base-rich soils, foremost the positively differentiating species *Rapistrum rugosum*, which showed yet another prominent flowering trait of a yellow *Brassicaceae*, and *Scandix pecten-veneris*. Furthermore, the group showed an association with various *Fabaceae*, such as *Vicia lutea*, *V. sativa*, *Lathyrus aphaca*, and *Melilotus indicus* (Table 2). The second main group included the most productive fields on the island, as indicated by high frequencies and abundances of nutrient-demanding species, such as *Glebionis segetum* and *Anthemis cotula*. Moreover, it was rich in plants considered speirochorous, such as *Agrostemma githago* and *Lolium temulentum* (Table 2), indicating widespread use of in-farm crop seeds.

Cluster 3: *Glebionis segetum-Ranunculus marginatus* community (Figure 4C). This community (45 plots) was associated with fields with intermediate to wet (seasonal) soil moisture, as indicated by high percentage frequencies

of the positively differentiating species *Ranunculus marginatus* (Table 2). The low number of high-constancy differential species suggested considerable heterogeneity within the community. Rather than the presence of particular species, this community is characterized by the absence of the specialized species typical of the second community in the group. In the main flowering season, the golden yellow flowers of *Glebionis segetum*, together with *Rapistrum rugosum*, were most striking. The fields of this cluster were mainly found in productive flatland areas with alluvial humus-rich soils around the villages of Kontias and Tsimandria and at the foot of volcanic hills on the Fakos peninsula (Figure 1; Figure 5). The area of Kontias–Tsimandria included fields with rather high agricultural intensity, application of synthetic fertilizer, and the cultivation of otherwise uncommon crops, such as triticale and *Triticum aestivum*. The community also hosted unwanted non-resident grasses, such as *Lolium multiflorum* and *Alopecurus myosuroides*, indicating foreign cereal seed import.

Cluster 4: *Hypericum triquetrifolium-Leontice leontopetalum* community (Figure 4D). This community (27 plots) was particularly noteworthy due to the occurrences of vanishing geophytes such as *Leontice leontopetalum* and *Gladiolus italicus*. The fields of this community were characterized by loamy and stony, base-rich soils. This was also indicated by a high number of positively differentiating species, such as *Sinapis arvensis*, *Hypericum triquetrifolium*, *Bifora testiculata*, *Rhagadiolus stellatus*, *Anagallis foemina*, and *Buglossoides arvensis* (Table 2). Though none of these mostly inconspicuous species showed a dominant flowering aspect, the unique appearance of *Leontice leontopetalum*, striking pink of *Gladiolus italicus*, and characteristic scent of *Bifora testiculata* were distinctive and occurred together with the yellow flowers of *Rapistrum rugosum*. The *Hypericum triquetrifolium-Leontice leontopetalum* community was found in the northern part of the Fakos peninsula and east of Portianou, where volcanic rock and tuff occur, and scattered in other parts of the island (Figure 1; Figure 5).

Environmental gradients across spring communities

The three-dimensional, unconstrained ordination (NMDS) revealed distinct ordination patterns among the four spring vegetation communities (stress = 0.189), supporting the ecological differentiation among them (Figure 6). The main gradient (NMDS axis 1) was correlated with the ecological indicator value reaction ($R^2 = 0.777$; $p < 0.01$; Table 3), separating communities along a soil pH gradient. The *Glebionis segetum-Ranunculus marginatus* and

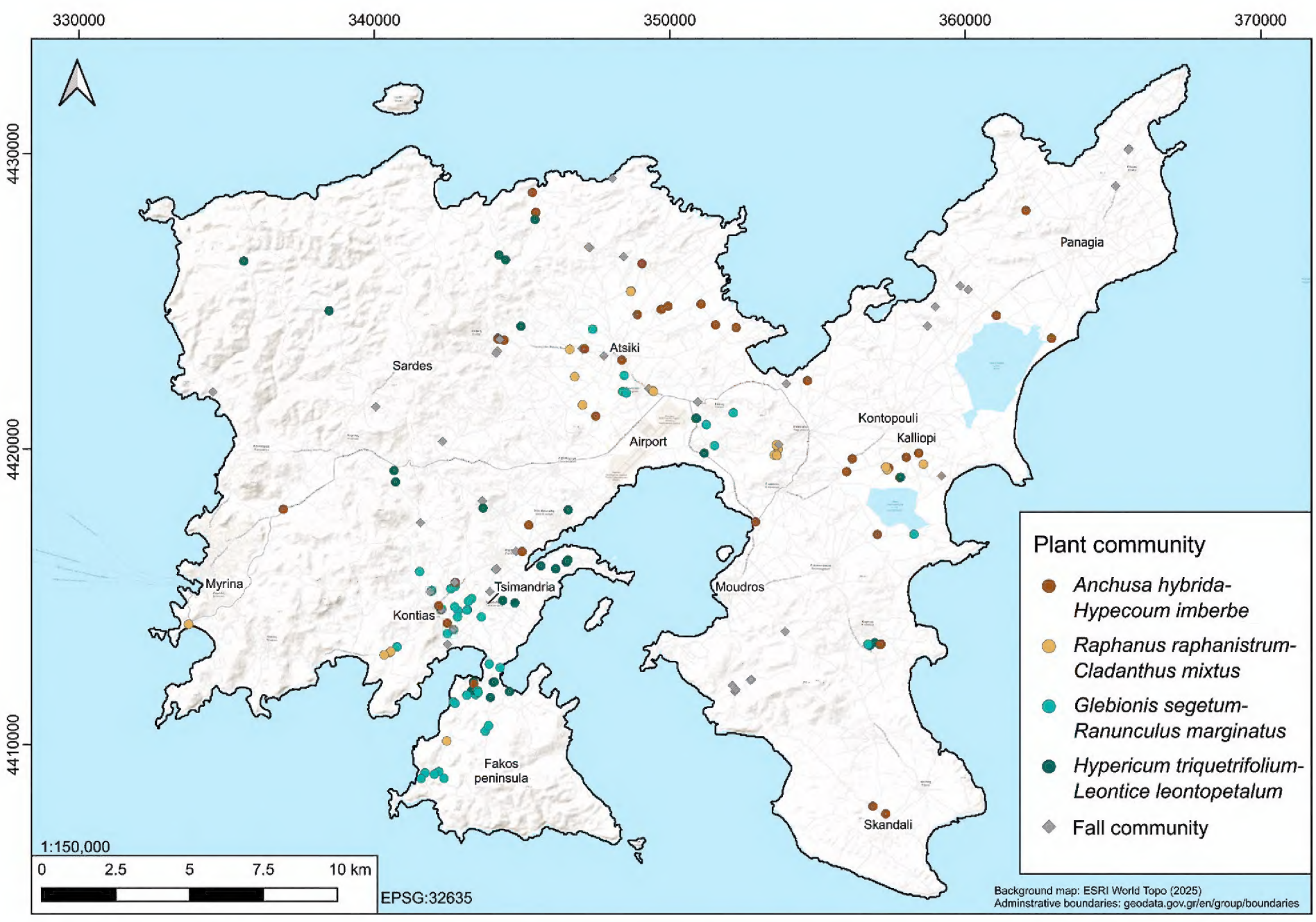

Figure 5. Map of Lemnos depicting the sampled locations and their classification into the four spring communities (*Anchusa hybrida-Hypecoum imberbe*; *Raphanus raphanistrum-Cladanthus mixtus*; *Glebionis segetum-Ranunculus marginatus*; *Hypericum triquetrifolium-Leontice leontopetalum*) and the fall community.

Hypericum triquetrifolium-Leontice leontopetalum communities were associated with higher reaction values, indicating more base-rich soils.

Additionally, axis 2 was marginally correlated with temperature (R^2 = 0.468; p = 0.059) and moisture (R^2 = 0.446; p = 0.063), suggesting higher moisture conditions within the *Raphanus raphanistrum-Cladanthus mixtus* and *Glebionis segetum-Ranunculus marginatus* communities and drier conditions in the *Anchusa hybrida-Hypecoum imberbe* and *Hypericum triquetrifolium-Leontice leontopetalum* communities (Figure 6).

Light and nutrients were not significant (Table 3). Altogether, the composition of the spring communities reflected a strong edaphic gradient primarily shaped by soil reaction and, secondarily, by soil moisture.

Table 3. Correlations with NMDS axes, coefficient of determination (R^2), and p-values of EIVE (reaction, temperature, moisture, light, and nutrient) fitted to the spring NMDS ordination (axes 1–3).

	NMDS1	NMDS2	NMDS3	R^2	p-value
R (reaction)	-0.782	-0.619	-0.067	0.777	0.001
T (temperature)	-0.379	-0.893	-0.241	0.468	0.059
M (moisture)	-0.079	0.903	0.422	0.446	0.063
L (light)	-0.151	-0.984	-0.089	0.198	0.517
N (nutrient)	-0.818	-0.495	0.294	0.094	0.818

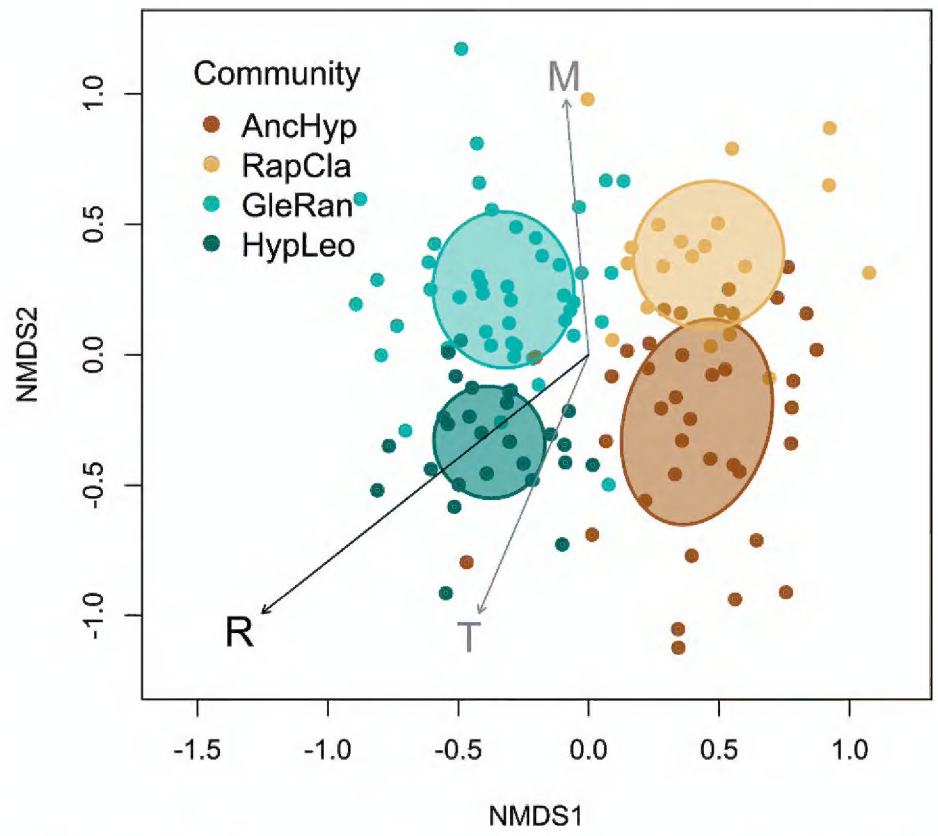

Figure 6. Three-dimensional NMDS ordination of spring plots (stress = 0.189). Sites are colored by community (AncHyp: *Anchusa hybrida-Hypecoum imberbe*; RapCla: *Raphanus raphanistrum-Cladanthus mixtus*; GleRan: *Glebionis segetum-Ranunculus marginatus*; HypLeo: *Hypericum triquetrifolium-Leontice leontopetalum*). The ellipses represent standard deviation around the centroid of each cluster. EIVE reaction (R), temperature (T), and moisture (M) were fitted post hoc with significant (p < 0.01) values in black and marginally significant (p < 0.1) values in grey.

Association between plant communities and indicator values

The community-weighted means of EIVE differed between plant communities (Figure 7). The plant community in fall was mainly characterized by a higher affinity for light and temperature. Reaction and nutrient values were also comparatively high while moisture was lower. The EIVE values of the spring communities reflected the results presented in the NMDS (Figure 6). Among the spring communities, the values of reaction and temperature were highest in the *Hypericum triquetrifolium-Leontice leontopetalum* community and lowest in the *Raphanus raphanistrum-Cladanthus mixtus* community. The affinity for moisture was highest in the *Raphanus raphanistrum-Cladanthus mixtus* and *Glebionis segetum-Ranunculus marginatus* communities. The values for light were a bit higher in the *Hypericum triquetrifolium-Leontice leontopetalum* community while nutrient values were highest in the *Glebionis segetum-Ranunculus marginatus* community.

Geological and soil variation across seasons and communities

Eocene-Oligocene molasse and Holocene alluvial deposits were the most frequent underlying geological substrates in the fields (Figure 8A). They varied significantly between communities (Chi-squared test, p < 0.01). Fields of the *Anchusa hybrida-Hypecoum imberbe* community were mostly located in areas with molasse and also alluvial deposits. The *Raphanus raphanistrum-Cladanthus mixtus* community showed a high affinity for volcanic rocks (20%) and tuffs (25%). Alluvial deposits were most common under fields of the *Glebionis segetum-Ranunculus marginatus* community (73%). The *Hypericum triquetrifolium-Leontice leontopetalum* community had the strongest association with molasse (41%) and tuffs (30%). Furthermore, the fields surveyed in fall were mainly distributed on Eocene-Oligocene molasse and Holocene alluvial deposits, with some found over volcanic rocks (Figure 8A).

Field and crop types across seasons and communities

The type of field crops varied significantly between communities (Figure 8B; Chi-squared test, p < 0.01). The most common crop was barley. It was most frequent in the *Hypericum triquetrifolium-Leontice leontopetalum* community (59%). Mixed crop fields, mainly maslin of barley and oat, were abundant as well, with at least 21% of fields in each spring community and a higher abundance (42%) in the *Glebionis segetum-Ranunculus marginatus* community. Fields with oat as the single crop were rare. Fields sown with pulses were most frequent in the *Anchusa hybrida-Hypecoum imberbe* community (34) and much less frequent in the other communities. Wheats (triticale, *Triticum durum*, and *T. aestivum*) were most frequently found in the *Raphanus raphanistrum-Cladanthus mixtus* community (20%), followed

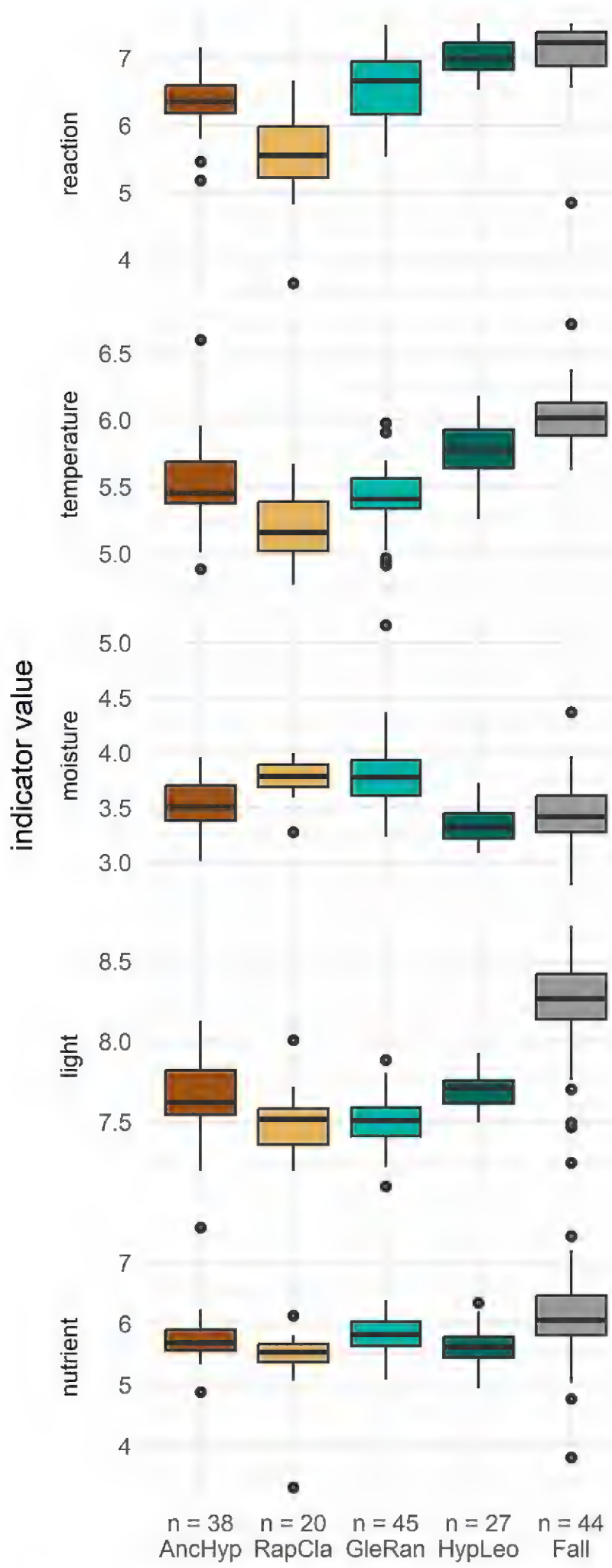

Figure 7. Boxplots depicting community weighted means of EIVE reaction, temperature, moisture, light, and nutrient for the four spring communities (AncHyp: *Anchusa hybrida-Hypecoum imberbe*; RapCla: *Raphanus raphanistrum-Cladanthus mixtus*; GleRan: *Glebionis segetum-Ranunculus marginatus*; HypLeo: *Hypericum triquetrifolium-Leontice leontopetalum*) and the fall community.

by the *Anchusa hybrida-Hypecoum imberbe* community (11%). Generally, the *Anchusa hybrida-Hypecoum imberbe* and *Raphanus raphanistrum-Cladanthus mixtus* communities had very different crop dominance in comparison to the other spring communities due to the high number of wheat fields and rotational fallows (10 to 13%). The fall community was mainly found on stubble fields (80%), with some fallows and fields sown with the summer legume crop *Vigna unguiculata* (Figure 8B).

Species richness in total and across seasons and communities

A total of 357 plant taxa were recorded, belonging to 47 families. The most common families were *Asteraceae* (69 species), followed by *Poaceae* (55), *Fabaceae* (49), *Caryophyllaceae* (18), *Plantaginaceae* (15), *Apiaceae*, and *Brassicaceae* (14). Species richness varied significantly between the seasons and was significantly higher in spring (mean = 26.6) compared to fall (15.6). It also differed significantly between the spring communities (Pairwise Wilcoxon test, $p < 0.05$; Figure 8C). The *Anchusa hybrida-Hypecoum imberbe* and *Raphanus raphanistrum-Cladanthus mixtus* communities exhibited lower richness (median ≈ 20 species/plot), while the *Hypericum triquetrifolium-Leontice leontopetalum* community had the significantly highest richness (median > 30), with a maximum of 62 species. Furthermore, stubble fields exhibited the lowest overall richness (mean = 13.3), while fields sown with pulses had the lowest richness among spring crop types (21.5). Other spring field types showed mean richness values between 26.7 and 30.0 species.

Occurrence of obligate agrestal plant species

The occurrence of obligate agrestal species, as defined by Bergmeier and Strid (2014), differed among the communities (Figure 8D). The fall plots showed a low occurrence of obligate arable species; however, research on autumnal arable plant communities is limited. The mean number of obligate agrestal species was highest in the *Hypericum triquetrifolium-Leontice leontopetalum* community, followed by the *Glebionis segetum-Ranunculus marginatus*, *Anchusa hybrida-Hypecoum imberbe*, and *Raphanus raphanistrum-Cladanthus mixtus* communities (Figure 8D).

We found a total of 33 wild obligate arable plant species. The most frequently found species were of least concern (LC), such as *Raphanus raphanistrum* (93 plots), *Rapistrum rugosum* (74), *Scandix pecten-veneris* (61), and *Sinapis arvensis* (55). More or less frequent country-wide near-threatened (NT) or vulnerable species were *Lolium temulentum* (54, VU), *Agrostemma githago* (50, NT), *Papaver hybridum* (31, NT), *Leontice leontopetalum* (19, VU), and *Anagallis foemina* (22, VU; Table 4).

Some vulnerable or near-threatened species were rare, such as *Adonis annua* (3 plots, NT), *Allium cyrilli* (1, VU), *Bupleurum subovatum* (2, VU), *Euphorbia falcata* (2, NT), *Glaucium corniculatum* (1, VU), *Linaria chalepensis* (1, NT), *Neslia paniculata* subsp. *thracica* (2, NT), *Vaccaria hispanica* (1, VU), and *Veronica triloba* (4, NT). Most of them were found in the fields of the *Hypericum triquetrifolium-Leontice leontopetalum* community (Table 4).

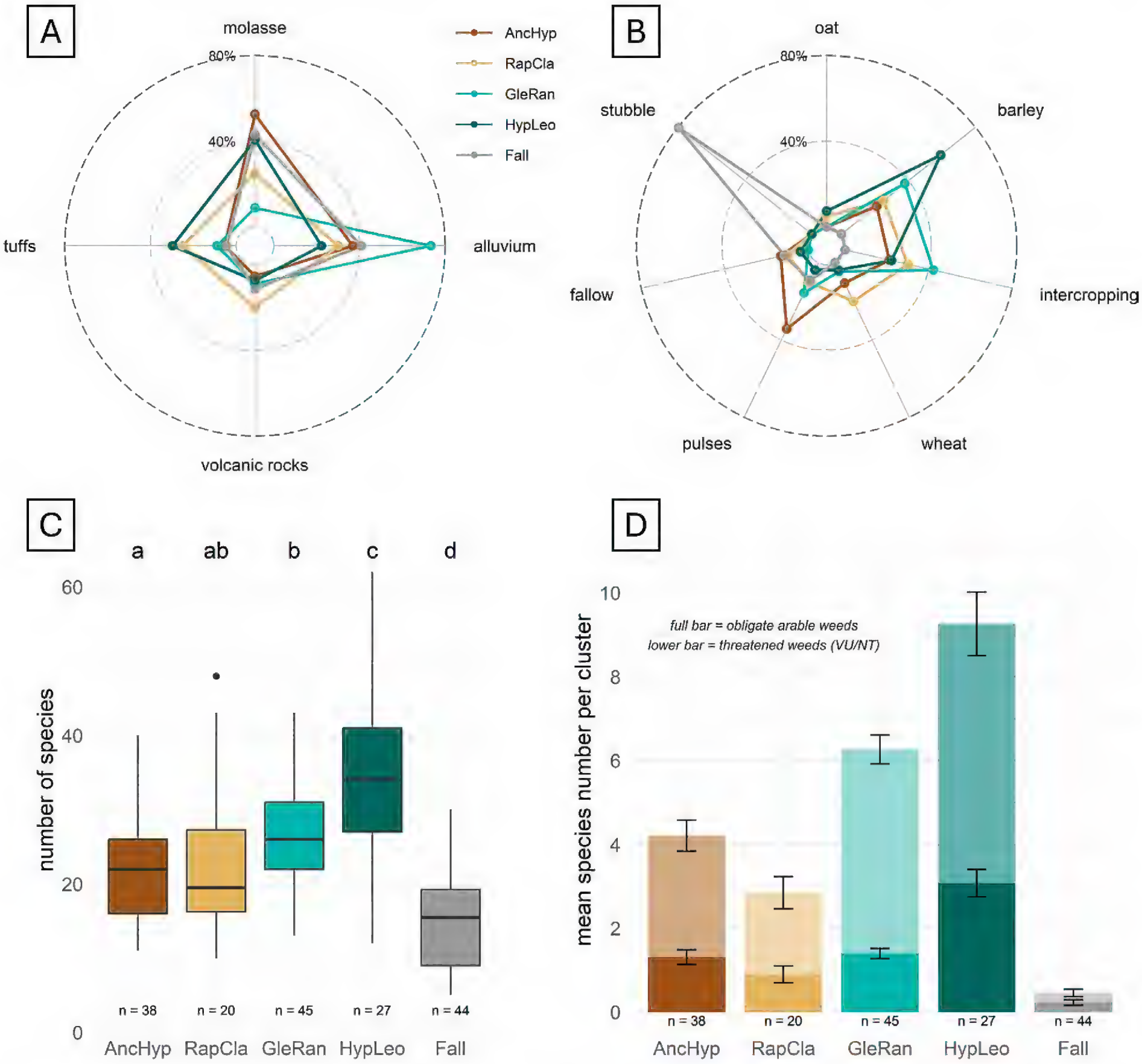

Figure 8. Characterization of plant communities in spring (AncHyp: *Anchusa hybrida-Hypecoum imberbe*; RapCla: *Raphanus raphanistrum-Cladanthus mixtus*; GleRan: *Glebionis segetum-Ranunculus marginatus*; HypLeo: *Hypericum triquetrifolium-Leontice leontopetalum*) and fall by: proportion of geological substrates (A), proportion of field and crop types (B), species richness (C), and mean number of obligate and threatened agrestal species (D). A: Percentage of geological substrates per community scaled 0–80%; B: Proportion of field/crop types per community, including fallows and stubble fields; other categories include oat (*Avena sativa*), barley (*Hordeum vulgare*), intercropping (mainly barley and oat or cereal-pulse mixes), *Triticum* species (triticale, *T. durum*, *T. aestivum*), and pulses scaled 0–80%; C: Boxplots showing species number per community with medians and significant differences (letters a-d, Pairwise Wilcoxon rank-sum test); D: Mean obligate agrestal species per cluster with error bars; full, transparent bars indicate mean per plot, lower bars show numbers of near-threatened (NT) and vulnerable (VU) species per plot.

Discussion

Our study presents the first comprehensive analysis of agrestal vegetation on an Aegean island and, apart from Crete (Bergmeier 2005), the first for any region in Greece. The less intensively managed winter-annual crop fields on Lemnos support a diverse range of agrestal species and different plant communities shaped by soil conditions and seasonal phases.

Spatio-temporal patterns of agrestal vegetation under less intensive management

Agricultural management practices and intensity influence the occurrence and composition of agrestal species (Mas and Verdú 2003; Fried et al. 2008; Cordeau et al. 2017; Alarcón Víllora et al. 2019). Less intensively managed agro-ecosystems promote species diversity and persistence of rare species (Armengot et al. 2011; Castro et al. 2016;

Table 4. Occurrence of obligate agrestal species on Lemnos, including the taxon name and threat categories (LC: Least Concern; NT: Near-Threatened; VU: Vulnerable) as identified by Bergmeier and Strid (2014) and their frequencies per spring (AncHyp: *Anchusa hybrida-Hypecoum imberbe*; RapCla: *Raphanus raphanistrum-Cladanthus mixtus*; GleRan: *Glebionis segetum-Ranunculus marginatus*; HypLeo: *Hypericum triquetrifolium-Leontice leontopetalum*) and fall communities, as well as total frequency.

Taxon	Threat category	AncHyp	RapCla	GleRan	HypLeo	Fall	Total
Adonis annua	NT	…	…	…	3	…	3
Agrostemma githago	NT	9	6	28	7	…	50
Allium cyrilli	VU	…	…	…	1	…	1
Alopecurus myosuroides	LC	1	…	5	…	…	6
Anagallis foemina	VU	6	…	2	10	4	22
Bifora testiculata	LC	…	…	7	13	…	20
Bupleurum subovatum	VU	…	…	…	2	…	2
Centaurea benedicta	LC	5	3	…	1	…	9
Consolida regalis subsp. *paniculata*	NT	1	…	…	2	4	7
Euphorbia falcata	NT	…	…	…	2	…	2
Fumaria parviflora	LC	4	…	…	…	…	4
Galium tricornutum	LC	3	1	18	17	…	39
Gladiolus italicus	LC	…	…	1	7	…	8
Glaucium corniculatum	VU	1	…	…	…	…	1
Glebionis segetum	LC	3	7	26	12	…	48
Hypecoum imberbe	LC	24	2	1	1	…	28
Lathyrus aphaca	LC	7	3	19	17	…	46
Legousia speculum-veneris	LC	…	…	…	1	…	1
Leontice leontopetalum	VU	3	…	…	16	…	19
Linaria chalepensis	NT	…	…	…	1	…	1
Lolium temulentum	VU	6	7	27	12	2	54
Medicago scutellata	NT	3	…	5	7	…	15
Neslia paniculata subsp. *thracica*	NT	…	…	…	2	…	2
Papaver hybridum	NT	19	5	1	6	…	31
Ranunculus arvensis	LC	…	…	1	5	…	6
Raphanus raphanistrum	LC	29	16	33	13	2	93
Rapistrum rugosum	LC	12	1	37	18	6	74
Scandix pecten-veneris	LC	6	…	32	22	1	61
Sinapis arvensis	LC	10	3	21	20	1	55
Vaccaria hispanica	VU	…	…	…	1	…	1
Veronica triloba	NT	1	…	1	2	…	4
Vicia lutea	LC	5	2	26	14	…	47
Vicia narbonensis	VU	3	…	2	4	…	9

Alarcón Víllora et al. 2019). Fields showing clear signs of herbicide use or intensive (synthetic) fertilization were excluded to focus on less intensively managed systems. Including such plots would likely dilute the soil-dependent plant community differentiation typical for less intensively managed agrestal ecosystems (Meyer et al. 2015). While detailed management data (e.g., timing and intensity of tillage, application of fertilizer) is lacking on Lemnos, the presence of maslin cereals and cereal/pulse intercropping, rotational pulses, fallow fields, and the use of in-farm crop seed, which promotes resown arable plant species, are characteristics of traditional, less intensive practices.

Under conditions of less intensive agriculture on Lemnos, seasonal phases are extant, and seasonality is the most important factor distinguishing arable plant communities. Most pronounced is the difference in species composition between spring plant communities in cultivated or fallow fields and the vegetation of stubble fields and autumnal fallow land. This reflects the differing life cycles and strategies of agrestal species.

Winter annuals flower in spring or early summer to set seed before harvest (Holzner et al. 1982). In contrast, species associated with fall plots germinate and flower later and exhibit growth forms and rooting strategies that allow them to survive or evade reaping and grazing of stubble fields. Traits such as low-lying buds, rosettes, prostrate stems, or below-ground storage organs enable these plants to persist vegetatively and grow once crops and early agrestal plants are removed. Additionally, their emergence or continued growth after harvest is economically insignificant and, apart from stubble field pasturage, not actively managed, allowing them to complete their life cycle and contribute to the seed bank (Bagavathiannan and Norsworthy 2012). This seasonal niche differentiation underlines the importance of the land-use rhythm and field phases for agrobiodiversity, in line with other studies from

Western and Central Europe (Lososová et al. 2004; Cimalová and Lososová 2009; Pinke et al. 2010; Bopp et al. 2022). In contrast, in large parts of Europe, stubble fields are plowed directly after the harvest, and there are no rotational fallows.

In less intensively farmed winter-cereal fields, we identified soil properties as the main drivers of plant community differentiation. We distinguished one group of communities on sandy, acidic soils and another on loamy, more base-rich soils with higher skeletal fraction. Moisture gradients contributed to additional differentiation in species composition. It is highly probable, although not proven by us, that the occurrence of moisture indicators varies annually and locally depending on the amount of winter rainfall. Similarly, edaphic factors, especially base content and soil texture, have been identified as the most important drivers for arable plant community differentiation under formerly less intensive agriculture in Europe (e.g., Hüppe and Hofmeister 1990; Lososová et al. 2004; Meyer et al. 2015; but see Fanfarillo et al. 2020b).

Species richness was higher on more base-rich soils, probably due to more favorable conditions for plant growth (Tyler 2003), but species composition varied between the four plant communities, with some species typically occurring on more acidic, unproductive fields. These findings highlight the role of soil heterogeneity in supporting biodiversity in agricultural systems (Hallgren et al. 1999; Fried et al. 2008).

The type of crop and time of sowing also influence the species composition of arable plant communities (e.g., Cimalová and Lososová 2009; Pinke et al. 2024). On Lemnos, the former depends on soil characteristics and farming requirements, the latter on weather fluctuations. Fallow land plays a key role in traditional crop rotation, aiming to enhance soil resilience by allowing periods of rest from cultivation. At the same time, fallows promote the local plant diversity, the abundance of floral resources, and the replenishment of soil seed banks (Castro et al. 2016), especially with low-impact tillage (Mas and Verdú 2003; Köllmann and Waldhardt 2022). In the historical rotation systems in temperate Europe, fields can alternate between winter-annual cereal and summer-annual cereal or root crop cultivation, whose arable plant communities differ significantly (e.g., Oberdorfer 1983). In contrast, the cultivation of summer crops is not envisaged in the meridional rotation system, as these would have to be irrigated and are therefore unsuitable in rainfed agriculture. The Mediterranean rotation stages (winter cereals, fallow, and winter legumes) therefore do not differ fundamentally in their species composition, as we were able to show on Lemnos.

Syntaxonomic affinity

All spring plots can be assigned to the class *Papaveretea rhoeadis* vegetation of arable crops in Eurasia and the Mediterranean region (Brullo et al. 2007; Mucina et al. 2016; Chytrý et al. 2024).

Within the *Papaveretea rhoeadis*, as an unpublished concept that was subsequently adopted by Brullo et al. (2020), Mucina et al. (2016) suggested the order *Gladiolo italici-Ridolfietalia segeti* as vegetation of arable crops in the Mediterranean. Of its four alliances, three have been defined to encompass winter-annual vegetation of arable crops (Nezadal 1989; Mucina et al. 2016):

- *Ridolfion segeti* contains the segetal vegetation on deep, loamy, or clayey soils.
- *Roemerion hybridae* can be found on mainly neutral or alkaline soils on base-rich, mostly calcareous substrates.
- *Rumicion bucephalophori* is limited to acidic, nutrient-poor soils.

Plant communities of these alliances have been described in parts of Western to Central Southern Europe (Portugal, Spain, France, Italy) and North Africa (e.g., Nègre 1978; Nezadal 1989; Ferro 1990; Deil 1997; Bardat et al. 2004; Brullo et al. 2007; Fanfarillo et al. 2019; Chakkour et al. 2023). Therefore, many of the diagnostic species used to define these alliances are rare or absent in the Eastern Mediterranean or show different habitat preferences, but several do occur in Greece and on Lemnos.

The *Anchusa hybrida-Hypecoum imberbe* and the *Raphanus raphanistrum-Cladanthus mixtus* communities resemble the *Rumicion bucephalophori*, described from the Iberian Peninsula (Nezadal 1989), and the more widespread *Scleranthion annui* (allocated to the *Aperetalia spicae-venti*). However, our communities share only a few differential species with those previously described, such as *Spergula arvensis* and *Cladanthus mixtus* (Nezadal 1989; Rivas-Martínez et al. 2002). Until a study on the vegetation of cereal fields on acidic and nutrient-poor soils in a geographically larger area is available, we provisionally favor a syntaxonomic affiliation of the first main group to the *Rumicion bucephalophori*.

The *Glebionis segetum-Ranunculus marginatus* community shows similarities to the *Ridolfion segeti*, supported by species such as *Phalaris paradoxa* and *Ranunculus marginatus* (Ferro 1990; Brullo et al. 2007). This alliance has been described as arable vegetation on thermo- to meso-Mediterranean deep heavy clay soils (vertisols) (Nègre 1978; Rivas-Martínez et al. 2002), resembling conditions in the fields of the *Glebionis segetum-Ranunculus marginatus* community on alluvial deposits of Lemnos, where we encountered deep cracks in the soil, typical of alternately shrinking and swelling soils with high amounts of expansive clay minerals. Kosmas et al. (2024) mapped them as fine- to medium-textured, deep to very deep soils, often poorly drained.

The *Sileno gallicae-Chrysanthemetum segetum* described for Crete (Bergmeier 2005) is most similar to the *Glebionis segetum-Ranunculus marginatus* community, mainly due to the constancy of *Raphanus raphanistrum* and *Glebionis segetum* (syn. *Chrysanthemum segetum*) and indicator species of soils with alternating moisture levels.

The *Hypericum triquetrifolium-Leontice leontopetalum* community differs strongly from the other communities

described on Lemnos due to its basophil character and aligns with the *Roemerion hybridae*. Diagnostic species of fields in Lemnos in common with West Mediterranean plant communities of this alliance (Nezadal 1989; Rivas-Martínez et al. 2002) are, among others, *Anagallis foemina*, *Bifora testiculata*, *Buglossoides arvensis*, *Galium tricornutum*, *Lathyrus aphaca*, and *Rapistrum rugosum*. They appear to be typical of base-rich (but not necessarily calcareous), often stony, deep, and dry soils in the wider Mediterranean region, far beyond the distribution area previously known from literature evidence. As our data show, the spectacular geophyte *Leontice leontopetalum* is a character species for the eastern Mediterranean subarea of the *Roemerion hybridae*. Further differential species of the alliance with high fidelity in the Lemnos dataset include *Hypericum triquetrifolium*, *Rhagadiolus stellatus*, and *Torilis nodosa*.

The plant community encountered on autumnal stubble and fallow fields emerges in summer on dry, sun-exposed fields on varying substrates with little competition. It is characterized by more ruderal than specialized agrestal plant species. The plant community has much in common with the alliance *Diplotaxion erucoidis* of the western and central thermo- and meso-Mediterranean regions, as defined by species such as *Chrozophora tinctoria*, *Dittrichia graveolens*, and *Heliotropium europaeum* (Rivas-Martínez et al. 2002). The *Diplotaxion erucoidis* has been classified in the class *Chenopodietea* or in the superclass *Stellarietea mediae* (e.g., Rivas-Martínez et al. 2002) until it was attributed to a newly described class, *Digitario sanguinalis-Eragrostietea minoris* (Mucina et al. 2016).

Further syntaxonomic studies across other Greek islands and mainland regions are needed to determine the distribution of these vegetation types and clarify the regional applicability of existing alliances.

Conservation of less intensively managed agro-ecosystems and their biodiversity

From an economic perspective focused on yield maximization, agrestal species are often regarded as weeds and generally unwanted due to expected yield losses, prompting the application of herbicides (Flessner et al. 2021). However, this overlooks their vital contributions to agro-ecosystem resilience and insect and bird biodiversity (Johnson et al. 2011; Mijatović et al. 2013; Landis 2017). Insect biodiversity is particularly important to sustain ecosystem services, such as pollination or biological control (Jankielsohn 2018; Magagnoli et al. 2024).

Populations of arable plant species, especially obligate specialists, have dramatically declined in many parts of Europe since the 1950s due to intensification of agricultural practices (Fried et al. 2010; Meyer et al. 2013; Richner et al. 2015). Furthermore, conventional mechanical tillage is the leading cause of soil degradation and decreases the productivity of the land, while tillage in conservation agro-ecosystems and fallowing increase soil resilience (Lal 1993; Castro et al. 2016; Derpsch et al. 2024).

Because of their specific requirements and adaptation to agricultural disturbance, agrestal plant species are dependent on traditional, low-impact agriculture (Bergmeier and Strid 2014). As indicators of community and ecosystem variation and soil health (Fanfarillo et al. 2020a), they offer insights into the sustainability of land management.

On Lemnos, the highest abundance of obligate arable plant species was associated with less intensively managed barley or maslin fields on loamy, base-rich soils. Soil variation enhanced community diversity by supporting different ecological groups of species. Furthermore, the integration of fallows and pulses in the crop rotation and in the agricultural landscape contributes to flowering plant abundance (Castro et al. 2016). This can be seen in the *Anchusa hybrida-Hypecoum imberbe* community which is, more than the other communities, associated with pulse fields and fallows and supports not only a high number of obligate arable plant species but also rich flowering attracting pollinators.

Because pollinators exhibit varying floral preferences, higher plant species diversity supports greater insect diversity (Nicholls and Altieri 2013; Sutter et al. 2017). In addition, the sequence of early and late flowering species, such as vernal aspects of *Anagallis* spp., *Anchusa hybrida*, *Cladanthus mixtus*, *Hypecoum imberbe*, *Papaver rhoeas*, *Rapistrum rugosum*, and others, and aestival aspects of *Dittrichia* spp., *Heliotropium europaeum*, and *Polygonum arenarium* provide continuous resources throughout the growing season.

This underlines the importance of the less intensive agricultural systems, still widespread on Lemnos, that sustain the biodiversity of arable plant species and their associated fauna. Fortunately, the Terra Lemnia project supports the conservation and restoration of Lemnos' agricultural practices, local animal breeds and landraces, the associated wild flora, and the promotion of local products (MedINA 2021). Therefore, the island is a positive example for a successful continuation of sustainable agricultural practices in contrast to the general pressure of agricultural intensification.

Conclusion

Our study provides the first comprehensive assessment of agrestal plant communities in Greece, apart from Crete (Bergmeier 2005). It reveals how less intensive agriculture with traditional land-use practices supports a rich and diverse flora. Seasonal phases with distinct vernal and aestival aspects, patterns, and communities emerged as the primary driver of floristic variation. Spring communities are further structured by considerable variation in soil texture, moisture, and productivity, reflecting strong edaphic filtering, and are additionally influenced by crop type. Our results highlight the occurrence of widespread as well as rare obligate agrestal species, several of which are threatened or declining, some even in a European-wide context (Bergmeier and Strid 2014). The persistence of these species underscores the ecological value of the island's less intensive field management and crop rotation practices.

Maintaining low-intensity farming with traditional practices and landscape patterns is vital for conserving wild arable plant species, the biodiversity depending on them, and associated ecosystem services (Storkey 2020). Lemnos exemplifies how low-impact agro-ecosystems can sustain high levels of biodiversity, including specialized taxa dependent on regular agricultural disturbance. As such, it represents a valuable reference system for conservation and agro-ecological planning. With unrestrained agricultural intensification across much of Europe, some countries start debating how to re-establish biodiversity-rich agricultural landscapes (Görzen et al. 2021). Although Lemnos has by no means remained unchanged over time, it has become an illustrative example for sustainable land use and a refuge for arable plant biodiversity in Mediterranean agricultural landscapes.

Data availability

The relevés collected and used in the present study are available in Suppl. material 1. They are currently processed for inclusion in EB's Segetal Weed Vegetation Database of Greece (EU-GR-004) and in the European Weed Vegetation Database (Küzmič et al. 2020).

Author contributions

EB and LR planned the research. EB and SM conducted the vegetation surveys with additions by LR in 2025. LR performed the statistical analyses and the manuscript, being supported by EB. All authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
R script (.qmd) used for the statistical analyses and R environment file (.RData) containing all data frames required to reproduce the analysis (compressed as .zip).
Link: https://doi.org/10.3897/VCS.164437.suppl1

Supplementary material 2
Full synoptic table and species matrix of the spring and fall communities (.xlsx).
Link: https://doi.org/10.3897/VCS.164437.suppl2

Supplementary material 3
Full synoptic table and species matrix of the four spring communities (.xlsx).
Link: https://doi.org/10.3897/VCS.164437.suppl3